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CONTENTS

PAGE

JOBLING, B. On two subspecies of *Culex pipiens* L. (Diptera) . . . . . 193–216, 8 figs.

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ON TWO SUBSPECIES OF *CULEX PIPIENS* L (DIPTERA)

By B. Jobling.

(*Wellcome Entomological Field Laboratories, Wellcome Bureau of Scientific Research, London.*)

(Read 1st June, 1938.)

With Eight Figures.

Contents.

	PAGE
Introduction	193
The eggs and their development	196
The first stage larvae	198
The second stage larvae	199
The third stage larvae	200
The fourth stage larvae	202
Some ecological factors and the development of the larvae	205
(*a*) Habitats of the larvae	205
(*b*) Temperature	207
(*c*) Salinity of water	209
The adults	211
References	215

Introduction.

It is now well established that in Europe, Palestine and Egypt the common *Culex pipiens* L. is represented by two forms, which, according to the investigations of several workers, differ biologically from each other as follows: One breeds near, or not very far away from houses, in the open, undergoes complete hibernation during the winter, cannot mate in a small space, does not attack man and before oviposition requires a blood-meal, which it obtains from birds, rodents and even frogs. The other breeds near, or inside, buildings, does not hibernate, can mate in a small space (small cages and jars), attacks man readily and also feeds on birds, but can lay fertile eggs without a meal.

The description of the man-biting mosquito was given a very long time ago, but its biological difference from the man-ignoring one has only been completely established in the last few years.

In 1775 Forskål described a new species of *Culex*, from Egypt. He wrote that it is of the size and shape of the common *Culex pipiens*, extremely abundant at Roseta, Cairo and Alexandria, and at night is disturbing to sleepers. The description of Forskål indicates that the species must have belonged to the genus *Culex*, and since, according to Kirkpatrick (1925), *Culex fatigans* Wiedemann is not present in Egypt, and there is no other species of this genus which attacks people inside houses at night, it can therefore be taken that Forskål's description refers to the man-biting *C. pipiens*. As regards Kirkpatrick's description of *C. pipiens*, it shows that this author was dealing with

two mosquitoes. Some parts of his description agree with the structure and the habit of the man-ignoring mosquito, whereas other parts of the same description fit perfectly the man-biting one.

Germar (1817) described a new species of *Culex* which he called *C. domesticus*. It is clear from his description of the habits of this mosquito in Dalmatia that this author was dealing with the man-biting *C. pipiens*.

The first description of the man-ignoring *Culex* was given by Ficalbi (1890), under the name of *C. phytophagus*. He pointed out that " the mosquito with which *C. phytophagus* may be, and commonly has been confused, is the common haematophagous mosquito which here I too have called *C. pipiens*." He gave the following comparative diagnosis of *C. phytophagus* and *C. pipiens* (p. 126) : " our common haematophagous mosquito is on the whole light in colour, *C. phytophagus* is on the whole darker . . . the dorsum of the thorax of *C. pipiens* approaches more to a light reddish almost rust colour, with golden down, whereas in *C. phytophagus* the thorax is of a dark cigar brown, with golden down . . . in *C. pipiens* the tibiae and the joints of the tarsi are darker than the femora it is true, but they do not approach black, whereas in *C. phytophagus* the tibiae and the joints of the tarsi are of a black brown and at the extremity of the tibiae a whitish-yellow spot is visible even to the naked eye. To all this must be added that *C. pipiens* is notorious as a blood-sucker, while *C. phytophagus* feeds on nothing but vegetable juices."

Ficalbi (1893) discussed the identity of *C. pipiens* of south and central Europe with that of Lapland. He pointed out that " If subsequent investigations show that the northern species [Lapland] is not identical with the common European haematophagus mosquito, then the name *pipiens* L. we shall leave to the northern species, and to the common haematophagus mosquito of Europe might be given the name *C. haematophagus*." In his other paper (1896) there is only the redescription of his *C. phytophagus*. It is seen from the writings of Ficalbi that he was not sure whether the man-biting mosquito, or the man-ignoring one, was identical with *C. pipiens* L. from Lapland.

Edwards (1921) included all the above-mentioned names in the synonymy of *C. pipiens* L. He was informed by Barraud that a different type of larvae of *C. pipiens* is present in Palestine and Syria, with the siphonal index 4·5. As regards these larvae, Edwards pointed out that if it is shown that the Palestine type of larva is identical with the larva of the widely distributed Mediterranean, troublesome race, then the varietal name *molestus* Forskål might be given to this form.

The first suggestion of the presence of the different races of *C. pipiens* was given by Grassi (1923). He indicated that it is the light-coloured mosquito which is very troublesome to man, but he did not establish completely the biological difference between the two races.

The first experimental evidence that *C. pipiens* can lay fertile eggs without a blood-meal was given by Neumann (1912), who bred several generations of this mosquito, feeding the adult females exclusively on sugar solution.

In 1929, Boissezon, Huff and Roubaud, independently of each other, found examples of *C. pipiens* which can breed without a blood-meal. But it was Roubaud (1930, 1931) who established the existence of the biological races of this mosquito. The man-biting, non-hibernating race he called " autogenous," because it could produce fertile eggs without a blood-meal, from the material accumulated by the adult during its larval period (Roubaud and Toumanoff, 1930). As this race could also mate in a very small space, he called it " stenogamus." The man-ignoring, hibernating race which required a blood-

meal before oviposition and a very large space for mating, he called " anautogenus " and " eurygamus."

After the discovery of the man-biting, autogenous race in France, it was found in Germany by Hecht (1932). The German strain from Elberfeld was introduced into the Wellcome Laboratory by MacGregor (1932). He found that under laboratory conditions its biology was similar to that of the French strain described by Roubaud. In the same year this mosquito was found by Vincent (1933) in Hungary, and by Tate and Vincent (1934) in Greece and Malta.

Roubaud (1933) gave a more complete account of the biology of the two races and named the man-biting, autogenous mosquito *C. pipiens autogenicus* and the man-ignoring, anautogenous one *C. pipiens pipiens* L.

It must be mentioned here that the earliest authors (Forskål, Germar and Ficalbi) based their separation of the man-biting mosquito from the man-ignoring one upon the difference in their coloration, while Roubaud used biological characters. The true morphological difference had not then been appreciated.

When Marshall and Staley (1935a) discovered the man-biting, autogenous mosquito near their laboratory at Hayling Island, they began to study its structure, and in their papers (1935b and 1935c) described several morphological characters by which it was possible to separate this mosquito from the man-ignoring, anautogenous one. They found that the fourth stage larvae of the man-biting mosquito have a smaller siphonal index and more branches in the siphonal tufts than those of the man-ignoring ones. As regards the adults, they found that the combined length of the first four segments of the palps of the male of the man-biting mosquito does not exceed the length of the proboscis (labium), whereas in the man-ignoring one the combined length of these segments is longer than the proboscis (labium), and that the number of hairs on the ninth tergite is greater in the former mosquito than in the latter.

As regards the morphological difference of all the stages of the larvae, I have shown (1936) that the form of the siphon and the length of the anal papillae are distinctly different in these two mosquitoes, and that by this character their larvae can be separated easily from each other in mixed culture.

In a later paper (Marshall and Staley, 1937) revised all the characters and by the examination of Réaumur's figures of *C. pipiens* (1738), to which Linnaeus referred in his description of this species, they established the fact that this name belonged to the man-ignoring, anautogenous mosquito. They suggested the elevation of the man-biting, autogenous mosquito to specific rank and called it *C. molestus* Forskål. Although some of the morphological characters, especially in the adults, are very distinct, this mosquito cannot be considered as a distinct species, because it has already been shown by Roubaud (1933), de Buck (1935), Weyer (1936) and by Tate and Vincent (1936) that cross-mating between it and the man-ignoring one produces fertile generations. It is also evident from the observations of Vincent (1933) in Hungary, and from the results of her subsequent experiments that mating of these mosquitoes with each other occurs in nature, when they live in the same place.

In the hybrid generation of these mosquitoes the characters intergrade and therefore the morphological gap, which should separate them, is absent. This intergradation of characters has been found in the larvae and adults which were bred from eggs received from Germany. These eggs must have been laid by a hybrid female, since after nine months of breeding this strain without a blood-meal, both larvae and adults acquired the morphological characters typical of the autogenous mosquito.

In their last two papers Marshall and Staley suggested the giving of varietal names to the different strains of the man-biting, autogenous mosquito. This, I think, is unnecessary, because, as far as is known, these strains do not differ biologically from each other and their morphological characters show considerable intergradation. It is quite possible that the same difference could be found in other species of Culicini, if they were studied more completely. In connection with this, I wish to mention here that when these characters were used for the separation of the strains of the British man-ignoring mosquito, it was found that the number of strains corresponded to the number of breeding-places from which the larvae were collected for examination.

This paper represents a comparative description of these two mosquitoes and also some additional data on their biology. Each mosquito is described here under its subspecific name. The man-ignoring, anautogenous mosquito is named *C. pipiens pipiens* L. and the man-biting, autogenous one *C. pipiens molestus* Forskål.

For the German strain of *C. pipiens molestus* I am indebted to Dr. W. Kikuth of Elberfeld, who was kind enough to send me several rafts of eggs. I wish to thank Professor P. A. Buxton of the London School of Hygiene and Tropical Medicine for the Grecian strain, Dr. O. Theodor of the University of Jerusalem for the Palestine strain and Mr. J. F. Marshall of the British Mosquito Control Institute for the British strain from Hull. I also wish to thank the librarian of the Wellcome Bureau of Scientific Research, Miss I. M. Bellis, for her translation of Ficalbi's papers. *C. pipiens pipiens* was studied from different places in Surrey. In calculating the siphonal index the length of the siphonal valve was not included in the length of the siphon.

The Eggs and Their Development.

It has already been found by previous workers that the egg-rafts laid by unfed females of *C. pipiens molestus* differ in shape from those of *C. pipiens pipiens*. According to Roubaud (1935) the egg-float of one subspecies differs from that of the other. It has also been noticed by Tate (see Marshall and Staley, 1936c) that the eggs of *C. pipiens pipiens* are much slenderer than those of *C. pipiens molestus*.

My own observations show that the egg-raft of the fed *C. pipiens molestus* also differs from that of the other subspecies. The raft of *C. pipiens pipiens* is a symmetrical structure, resembling a very minute boat. It is formed of numerous eggs which are arranged vertically in straight rows. One or two median rows are the longest and extend from one narrow end of the raft to the other. Each subsequent row is shorter than the preceding one, so that the lateral rows are the shortest. The number of eggs varies very much in different rafts. It has been observed that the size of a raft mainly depends upon the size of a female; the big females usually take the largest meals, and therefore lay the largest rafts. The largest raft, which has been found this summer, contained 505 eggs and the smallest 77 eggs. These small rafts are extremely rare. The majority of rafts contain from 150 to 300 eggs.

The arrangement of the eggs in the rafts of *C. pipiens molestus* is not so regular as in those of *C. pipiens pipiens*; in many rafts the eggs do not form rows at all. In almost every raft laid by this subspecies there is a number of eggs arranged obliquely. The form of the raft varies greatly: it may be rounded, square, triangular, oblong, ribbon-like, or of some indefinite shape, with a few eggs attached to its main part. The oblong and the triangular rafts are generally

laid by fed females. A count of the eggs in 120 rafts laid by unfed females gave the following figures: maximum 111, minimum 7, mean 43. In 52 rafts laid by fed females of the different broods, the corresponding figures were 176, 67 and 91.

As regards the development of the eggs of *C. pipiens pipiens*, in most rafts all eggs hatch. Of 21 rafts examined, 16 gave 100% development, one 55%, one 93% and the rest 95%. The percentage of development of eggs in the rafts laid by fed females of *C. pipiens molestus* is much lower than in those of the first subspecies. Thus, out of a hundred rafts laid by unfed females of this subspecies, only three rafts gave 100% development, the eggs of two rafts did not develop at all and the mean development was 74%. In the 35 rafts laid by fed females, 100% development was found in four rafts, the minimum was 3·7% and the mean 81%. This shows that the eggs laid by unfed females have a smaller percentage of development than those laid by fed ones.

In order to find out the duration of the egg stage in these subspecies, a raft of eggs of the same age from each mosquito was introduced into the same dish, and kept at a varying temperature which was taken twice daily. After the hatching of the eggs, the larvae of one subspecies were separated from those of the other by the morphological character of their siphon. The following table shows the results of these experiments.

Table 1.

Temperature of water			Duration of development of eggs in hours	
min.	max.	mean	*C. p. pipiens*	*C. p. molestus*
21·5	23·5	22·6	48	48
21·0	24·0	22·3	48	48
19·0	22·5	20·5	48	48
18·5	22·0	19·8	48	48
14·5	20·5	17·0	72	72
16·0	19·0	17·0	72	72
13·5	18·5	16·0	72	72
10·5	19·5	15·4	72	72
12·0	16·0	14·0	73	120
8·5	14·0	11·7	120	156

Between the mean temperature 22·6° C. and 19·8° C. the duration of the egg stage lasts 48 hours in both subspecies, between 17·0° C. and 15·4° C. duration is 72 hours, below 15° C. duration in the subspecies becomes different. At the mean 14·0° C. the eggs of *C. pipiens pipiens* take approximately the same time to develop as at higher temperatures, whereas the eggs of *C. pipiens molestus* take 47 hours longer. At a still lower temperature, when the mean was 11·7° C., the egg stage of *C. pipiens pipiens* lasted 120 hours, while in *C. pipiens molestus* it lasted 156 hours. The duration of the egg stage of *C. pipiens molestus* increases sharply when the mean temperature drops below 15·4° C., whereas in *C. pipiens pipiens* this increase appears at a lower temperature. This shows that below 15·4° C. the temperature becomes less favourable to the development of the eggs of *C. pipiens molestus* than to those of *C. pipiens pipiens*. The results of these experiments agree with those of Tate and Vincent (1936). These authors found that the eggs of *C. pipiens pipiens* are much more resistant

to the low temperature than those of the Hungarian strain of *C. pipiens molestus*.

The First Stage Larvae (fig. 1).

With the exception of the structure of the siphon and a very slight difference in the length of the anal papillae, the first stage larva of one subspecies does not differ from that of the other. In the larvae of this stage, towards the end of the first day, or on the second day after hatching, two-thirds of the distal part of the siphon becomes pigmented. In *C. p. pipiens* the edge of this pigmentation is ragged and dark, whereas in *C. p. molestus* it is not sharply indicated. The siphon of the larvae of both subspecies is divided by a slight constriction into

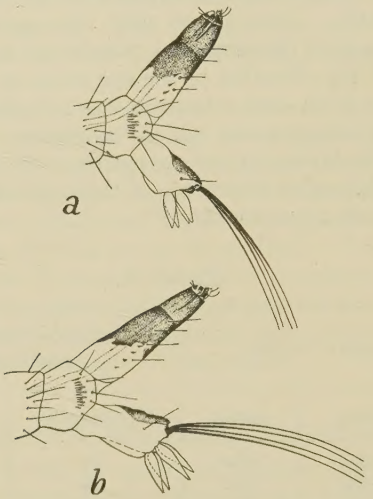

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Fig. 1.—*a*, Posterior end of abdomen of first stage larva of *C. pipiens molestus* Forsk.; *b*, same of *C. pipiens pipiens* L. × 75.

two parts : a distal one which is about one-third of the length of the siphon and a proximal one which represents the rest of the siphon. In *C. p. pipiens* (fig. 1, *b*) the distal part is funnel-shaped and the proximal is convex ventrally and slightly concave dorsally, in the middle, whereas in the German and Grecian strains of *C. p. molestus* (fig. 1, *a*) the distal part is dilated and the proximal part is slightly concave ventrally and convex dorsally. Table 2 shows the siphonal index and the length of the siphon in both subspecies.

Table 2.

	No. of larvae	Siphonal index			Length of siphon in μ		
		min.	max.	mean	min.	max.	mean
C. p. pipiens . .	60	3·0	4·1	3·6	266·5	348·5	310·8
C. p. molestus . .	60	2·5	3·0	2·7	209·1	299·3	265·5

It is seen from this table that the siphonal index and the length of the siphon are smaller in *C. p. molestus* than in *C. p. pipiens*. However, these characters intergrade and are not so reliable for the separation of the larvae as the form of the siphon.

The Second Stage Larvae (fig. 2).

The siphon of this stage larva of *C. p. pipiens* is slender, gradually narrowing towards the distal end and having a very slight sigmoid curvature (fig. 2, *b*). Its ventral side is slightly concave in the basal part, whereas the dorsal side is convex in the basal half and concave distally.

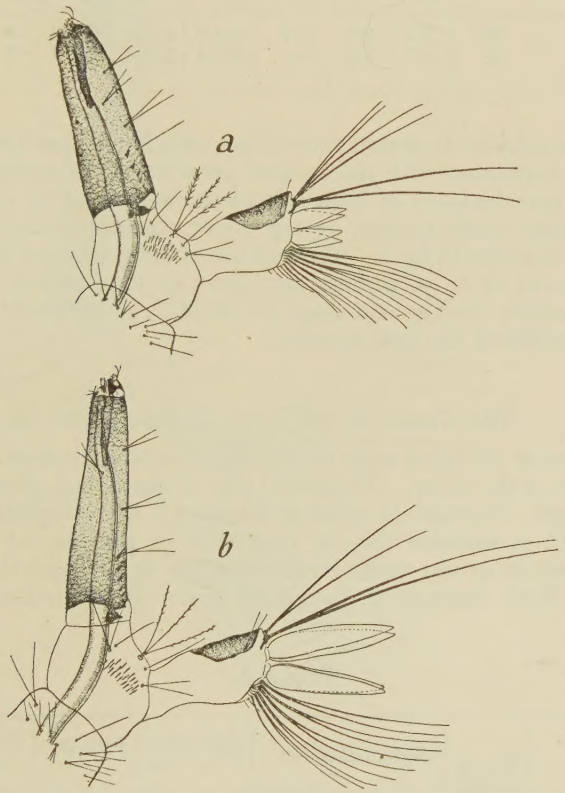

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Fig. 2.—*a*, Posterior end of abdomen of second stage larva of *C. pipiens molestus* Forsk.; *b*, same of *C. pipiens pipiens* L. × 60.

The siphon of *C. p. molestus* is distinctly different (fig. 2, *a*). It is stout and almost straight. Its ventral side is straight, except the most distal part, which bends inwards, the dorsal side is slightly wavy.

It may be seen from Table 3 that in *C. p. molestus* the siphon is shorter and the siphonal index is lower than in *C. p. pipiens*. The siphonal index of the second stage larva of one subspecies does not intergrade with that of the other.

Other characters in which the larvae differ from one another are the number of branches in the anal brush and the length of the anal papillae. The former character intergrades, and the latter is reliable only when the larva of both subspecies live in the same place, or in different places which have the same

Table 3.

	No. of larvae	Siphonal index			Length of siphon in μ			No. of branches in anal brush		
		min.	max.	mean	min.	max.	mean	min.	max.	mean
C. p. pipiens .	60	3·5	3·9	3·7	434·8	572·5	473·8	8	13	10·2
C. p. molestus .	60	2·7	3·3	3·0	426·4	508·4	457·2	9	19	13·0

concentration of salts in the water, since it has been found that the length of the anal papillae is correlated with the osmotic pressure of the water in which the larvae live. When the larva of both subspecies were bred in hay infusion or dog-biscuit infusion made in rain, or tap water, the appearance of their anal papillae was as is shown in fig. 2. The papillae of both wild and laboratory bred second stage larvae of *C. p. pipiens* are about as long as the anal segment, whereas in laboratory bred second stage larvae of *C. p. molestus* they are about as long as the saddle of the anal segment.

The Third Stage Larvae (figs. 3 and 4).

The structure of the third stage larvae of one subspecies does not differ very much from that of the other. The dorsal side of the siphon of both subspecies is almost straight, whereas the ventral side has a more regular curvature in the siphon of *C. p. molestus* than in that of *C. p. pipiens*. A more distinct difference is present in the ventral valves of the siphon and in their stirrup-shaped lever. Each valve of *C. p. pipiens* is double-pointed when examined

Table 4.

	No. of larvae	Siphonal index			Length of siphon in μ			No. of branches in anal brush		
		min.	max.	mean	min.	max.	mean	min.	max.	mean
C. p. pipiens										
Esher strain .	90	3·7	4·2	3·9						
Weybridge strain	90	3·4	4·4	3·9						
	180	3·4	4·4	3·9	703·0	925·0	810·3	16	36	24·5
C. p. molestus										
Grecian strain .	60	2·9	3·6	3·2						
German strain .	60	3·0	3·7	3·2						
	120	2·9	3·7	3·2	610·5	925·0	746·0	28	47	35·6

laterally. The ventral edge of the lever is almost straight and the dorsal one is broadly incurved. The valves of *C. p. molestus* are more or less triangular and broadly pointed when examined laterally. The ventral edge of the lever of this subspecies has a rounded projection in the middle and its dorsal edge is more narrowly incurved than that of *C. p. pipiens*.

In Table 4 the value of the siphonal index is given for two strains of each subspecies separately. As regards the index of the German and the Grecian

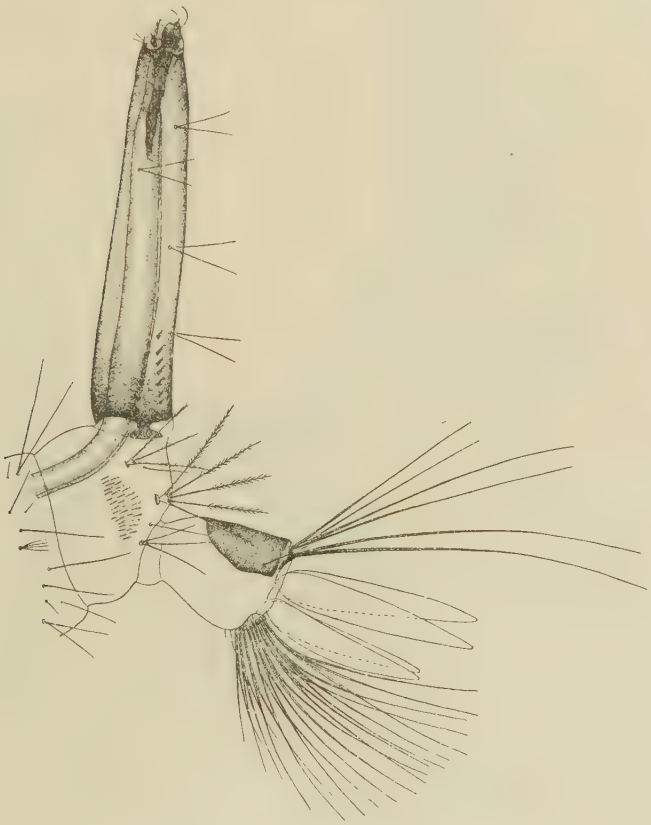

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FIG. 3.—Posterior end of abdomen of third stage larva of *C. pipiens pipiens* L. × 50.

strain of *C. p. molestus*, there is practically no difference at all, and the same is true of the two strains of *C. p. pipiens*. It is seen from the same table that the siphon is longer and its index is higher in *C. p. pipiens* than in *C. p. molestus*, but in the last-named subspecies there are more branches in the anal brush.

It is not easy to separate the third stage larva of one subspecies from that of the other by the above-mentioned two characters, but if they are living in the same place, or in different places, but with the same concentration of salts in the water, they can be easily separated by the character of their anal papillae. The

papillae of third stage larvae of *C. p. pipiens* are very much longer than the anal segment, especially the dorsal pair, whereas in larvae of *C. p. molestus* they are much shorter than the anal segment.

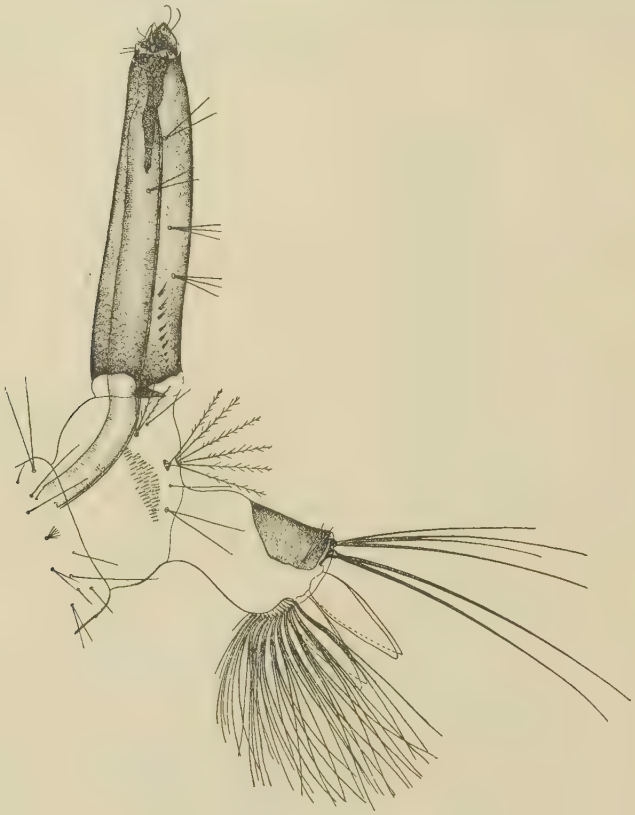

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Fig. 4.—Posterior end of abdomen of third stage larva of *C. pipiens molestus* Forsk. × 50.

The Fourth Stage Larvae (figs. 5 and 6).

In fourth stage larvae of these subspecies there is a slight difference in the number of the teeth of the mentum. The count of the teeth in 35 larvae of *C. p. pipiens* gave the following figures : minimum 14, maximum 24, mean 18; while in the same number of larvae of *C. p. molestus* the corresponding numbers were 18, 24 and 21. The large median tooth of the mentum was not included in these counts.

The best character of this stage larvae was also found in their siphon and the anal papillae. The siphon of the fourth stage larva of *C. p. pipiens* resembles that of the second stage larva. It is slender, gradually narrowing towards the distal end, and has a slight sigmoid curvature which is much more distinct in the basal part. In this part of the siphon the ventral surface is concave and the dorsal one is convex.

The siphon of *C. p. molestus* is shorter and broader than that of the other subspecies and does not show the sigmoid curvature. Its ventral side resembles that of *C. p. pipiens*, but the dorsal one is nearly straight.

Each ventral valve of the siphon of *C. p. pipiens* is roughly rectangular, with a blunt apex when examined laterally, whereas the valves of *C. p. molestus* are more or less triangular, with a rounded apex. The lever of the valves of

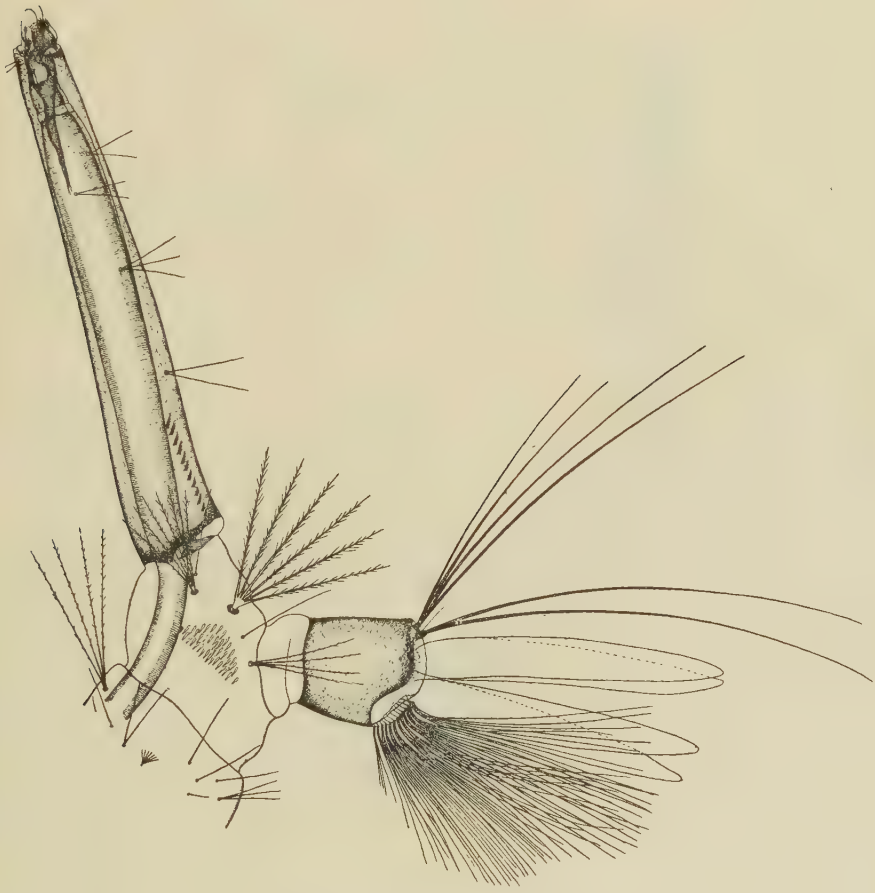

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Fig. 5.—Posterior end of abdomen of fourth stage larva of *C. pipiens pipiens* L. × 37·5.

C. p. pipiens narrows more or less uniformly towards the distal end which is curved, whereas in *C. p. molestus* it narrows abruptly in two places and its narrow distal part is straight. The anal papillae are again quite different in this stage when the larvae are bred in the same infusion. They are more than twice as long as the anal segment in *C. p. pipiens* and are shorter than the anal segment in *C. p. molestus*.

In Table 5 different figures are calculated for the four strains of *C. p. pipiens* and for the same number of strains of *C. p. molestus*. It shows that in the fourth stage larvae of *C. p. molestus* the siphonal index is smaller and the siphon is shorter than in *C. p. pipiens*, but in the latter there is a smaller number of branches in the anal brush than in the former. Although the mean values of these characters differ in the two subspecies, they intergrade in other parts of their range.

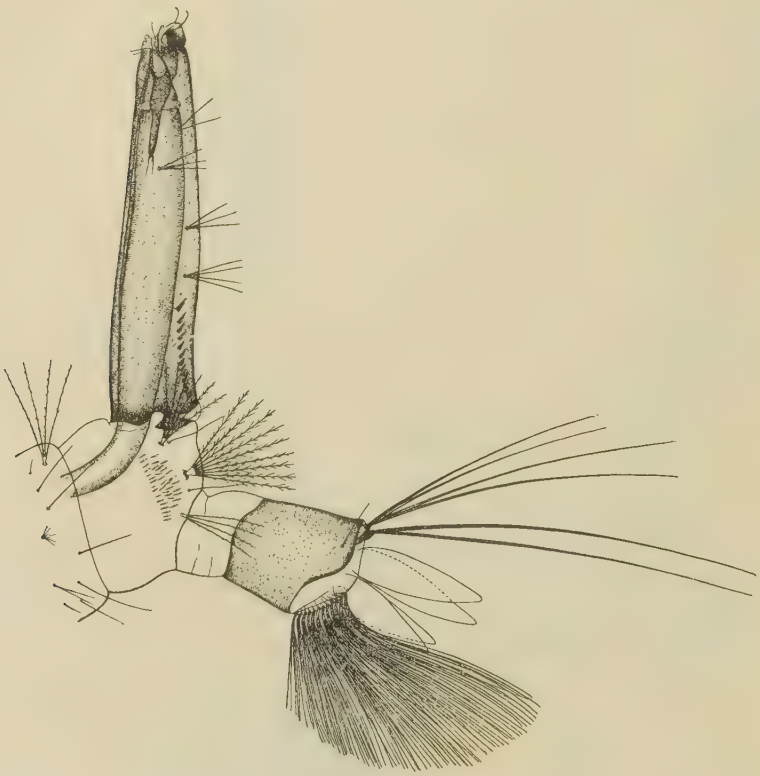

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Fig. 6.—Posterior end of abdomen of fourth stage larva of *C. pipiens molestus* Forsk. × 37·5.

Table 5.

	No. of larvae	Siphonal index			Length of siphon in μ			No. of branches in anal brush		
		min.	max.	mean	min.	max.	mean	min.	max.	mean
C. p. pipiens .	415	4·5	6·4	5·3	1184·0	1850·0	1573·8	41	79	60
C. p. molestus .	362	3·5	4·8	4·2	1110·0	1554·0	1329·0	59	90	70·5

In Table 6 the siphonal index and the number of branches of the siphonal tufts are given for each strain separately. It may be seen from this table that the mean value of the siphonal index of the Weybridge strain of *C. p. pipiens* does not differ very much from that of the British strain of *C. p. molestus*. The smallest siphonal index was found in the Palestine strain of *C. p. molestus*. However, I think that this figure does not represent the actual index of the

Table 6.

	No. of larvae	Siphonal index			No. of branches in siphonal tufts		
		min.	max.	mean	min.	max.	mean
C. p. pipiens							
Oxshott Common strain	25	5·1	6·4	5·7	8	14	10·2
Wisley „	60	5·0	5·9	5·6	8	14	10·8
Weybridge „	80	4·5	5·6	4·9	8	18	9·8
Esher wild „	80	5·0	5·9	5·5	8	15	11·0
„ from raft A . .	44				9	18	12·1
„ „ B . .	86	4·8	5·7	5·2	8	16	10·1
„ „ C . .	40				8	19	11·2
C. p. molestus							
British strain . .	44	3·9	4·8	4·4	10	19	12·9
Palestine „ . .	60	3·5	4·7	3·9	10	19	13·0
Grecian „ . .	118	3·6	4·8	4·2	8	13	9·7
German „ . .	140	3·8	4·7	4·2	8	15	10·9

Palestine type of larva, because it is quite possible that all these larvae were bred from eggs of the same raft. The siphonal index of different broods of the same strain may vary, as is shown by the Esher wild larvae and those which were bred from rafts A, B and C. As regards the branches of the siphonal tufts, in many larvae their number is not the same on both sides of the siphon. This character intergrades more than the others. For instance, the number of branches of the siphonal tufts is practically the same in the Wisley strain of *C. p. pipiens* and the German strain of *C. p. molestus*, and also in the Weybridge strain of *C. p. pipiens* and the Grecian strain of *C. p. molestus*. This shows that the siphonal index and the siphonal tufts have no specific value in these two mosquitoes.

Some Ecological Factors and the Development of the Larvae.

(a) *Habitats of the Larvae.*

Before the discovery of the two subspecies of *C. pipiens*, it was considered that this mosquito could breed in a great variety of habitats, ranging from clean water to the highly polluted liquid of cesspits. It was observed in France by Legendre (1931a, 1931b and 1932) that *C. pipiens* which has a light-coloured thorax and attacks man, breeds in cesspools, whereas that which has a darker thorax and does not attack man breeds in clean, surface water. Roubaud and Gaschen (1932) also indicate that in France *C. p. pipiens* breeds in more or less clean water, whereas *C. p. molestus* prefers the very polluted water of cesspools and septic tanks. They found that the larvae of *C. p. molestus*

are more resistant to a solution of human urine and ammonium carbonate than those of *C. p. pipiens*.

I have also observed that the larvae of the autogenous subspecies develop better and produce larger mosquitoes when the infusion is made from organic matter, is very turbid and is of a very cloudy appearance than when it is almost clear. As *C. p. molestus* is more common in the Mediterranean regions, and can breed in water of a very high degree of pollution, it is probable that the larvae, which were found in some cesspits in Palestine by Buxton (1924) and in almost every cesspit in Cairo by Kirkpatrick (1925), were of this subspecies.

The larvae of *C. p. pipiens* develop better when the infusion is less charged with fermenting organic matter. In highly polluted water there is usually a very high mortality amongst the last stage larvae and pupae. According to observations in this country, this subspecies prefers rain water for its breeding to the water of ponds and ditches. In the breeding season the larvae can be found in every unscreened rain-water tub and tank in the suburbs and in rural areas, but at the same time they may be completely absent from a very close-by pond. After several years of observations on the breeding of this mosquito, I came to the conclusion that many more rafts are laid immediately after prolonged rain followed by very warm quiet weather. A very heavy precipitation usually increases the number of breeding-places either by changing the conditions in the already existing water by dilution, or by filling up the dried ditches and depressions in the ground. It has been found that after the heavy rains in spring, the breeding-places of *Theobaldia morsitans* (Theob.) and of *Aëdes punctor* Kirby may become inhabited by larvae of *C. p. pipiens*.

An interesting case of this succession has been observed in a small pond on Arbrook Common. In the springs of 1934 and 1935 this pond was a very good breeding-place of *T. morsitans* and of *A. punctor*. The following spring, owing to the rainy weather, the water area of this pond was more than doubled, and the larvae of the above-mentioned mosquitoes were absent, but those of *C. p. pipiens* were very numerous. Last spring the pond did not overflow its banks, and larvae of *C. p. pipiens* were absent, but those of *T. morsitans* and of *A. punctor* were again very common.

In order to find out whether the conditions of water from the habitat of *T. morsitans* and of *A. punctor* are unsuitable for the breeding of *C. p. pipiens*, two glass jars were filled with water from the breeding-place of these two mosquitoes. Into each jar were introduced a few first and second stage larvae of *T. morsitans* and of *A. punctor* and a small raft of eggs of *C. p. pipiens*. During the course of this experiment the water of each jar was changed twice every week. By the end of April all the larvae of *T. morsitans* and of *A. punctor* had produced normal adults, but not a single larva of *C. p. pipiens* had developed to the adult stage. They started to die a few days after hatching, and only a few reached the third stage in their development.

It seems to me that the chief cause of mortality of *C. p. pipiens* was unsuitable food. The larvae of this mosquito feed almost exclusively on small particles of organic matter and plankton. They do not select their food, but swallow everything that is swept into their mouth by the action of their mouth brushes. Thus, if the larvae of this mosquito are placed in a suspension of indian ink, or carmine, or ground rotten leaves, their alimentary canal, in a short time, becomes filled with particles of these substances.

The water of the natural habitat of larvae of *C. p. pipiens* is either clean or turbid and its plankton is chiefly composed of bacteria and ciliata. On the

other hand, the habitat of larvae of *T. morsitans* and of *A. punctor* are temporary or permanent collections of water, which are usually of a very weak tea colour and are rarely turbid. The plankton of these collections of water resembles that of bog pools. It consists, besides bacteria, of a few ciliata and conjugata, many Desmidiaceae and Rotifera. The last-named organisms are sometimes present in enormous numbers. In the habitat of these two mosquitoes, the larvae of *C. p. pipiens* will receive different organisms as food, and probably also different types of organic matter and colloids from those of their natural habitat.

It was noticed that all the larvae of *C. p. pipiens* that have been bred in water from the habitat of those two mosquitoes, had an exceedingly long peritrophic membrane. In normally developing larvae this membrane extends, as a very thin-walled tube, through the mid gut and the narrow portion of the hind gut to the rectum. But in these larvae it protruded from the anus, and in some of them the protruding portion of it exceeded their own length. This excessive formation of the peritrophic membrane was probably induced by the unsuitable food, which stimulated the secretion of the glandular cells in the cardiac region of the alimentary canal of the larvae. The same condition of the peritrophic membrane has been found in many emaciated larvae from very polluted, green-coloured water from a tub, on a farm, and in larvae which were bred experimentally in dung infusion.

It is very often stated that this subspecies prefers to breed in water which is contaminated with manure. Though the larvae have often been found in contaminated water, it does not indicate that the breeding started when the water was in this state. It is more likely that the female laid the eggs when the water was in a different condition. It must be remembered that in a small amount of water, the conditions may be completely altered in a few days, especially during very warm or very rainy weather.

The experiments with dung infusion proved that it is not a suitable medium for the breeding of this subspecies. These experiments were arranged as follows: a raft of eggs was divided into two equal parts. One part of the raft was placed in dog-biscuit infusion and the other in dung infusion. After the introduction of the eggs, both jars were kept at the same temperature, and the appearance of the different stages of development was recorded. In the first experiment all the eggs in the dog-biscuit infusion developed to the adult in 19 days, while in the dung infusion the development was only 8·3% and its duration was 32 days. In the second experiment the percentage of development in the dog-biscuit infusion was 93·0, and the last mosquito appeared on the 21st day after the introduction of the eggs, whereas in the dung infusion the duration of development was 35 days and the percentage of development was only 3·6. The pH of the dung and the dog-biscuit infusions was 7·4 and 8·0 respectively. In these experiments the first and the second stage larvae appeared at the same time in both infusions, but the third stage larvae of the dung infusion appeared later than the fourth stage larvae in the dog-biscuit infusion. The appearance of the fourth stage larvae in the dung infusion was much later than that of the adults in the other infusion. The mortality among the larvae of the dung infusion occurred after they reached the second stage, but the greatest number of them died in the third and fourth stages.

(b) *Temperature.*

An attempt was made to discover experimentally the influence of temperature on the development of the larvae of both subspecies (Table 7). As the dog-biscuit infusion gave better results than any other infusion, it was used in all

the experiments. With the exception of experiments 1, 3 and 4, the rafts of both subspecies were placed in the same jar, so that, except in these three experiments, all the stages of development were in exactly the same condition. The temperature was taken twice a day and at the same time all the cast skins of the developing larvae were collected and identified. In the first experiment the range of temperature was 5° C., in the following six 9·5° C. and in the last two 6° C.

It may be seen from the table that between the mean temperature of 14·4° C. and 27·8° C. there is practically no difference between the duration of the different stages and the appearance of the first and the last adults of *C. p. pipiens* and those of *C. p. molestus*. When the mean temperature was 13·5° C. and 12·5° C. all the larvae of *C. p. pipiens* died in the second stage, while those of *C. p. molestus* began to die soon after hatching, and none of them reached the second stage. This seems to show that the larvae of these two subspecies are affected differently below 14° C. The smaller percentage of development of *C. p. pipiens* was probably produced by the high concentration of fermenting organic matter in the infusion. It has already been indicated that the development of the larvae of this subspecies proceeds better when the infusion is not too strong.

Table 7.

Appearance of the different stages in days and the percentage of development in the two subspecies. 1, four stages of larva; P, pupa; A, appearance of the first and the last adult.

No. of expts.	Mean temp.	*C. p. pipiens*							*C. p. molestus*						
		1^1	1^2	1^3	1^4	P	A	%	1^1	1^2	1^3	1^4	P	A	%
1	27·8	1	3	5	7	10	12–16	34·3	1	5	7	9	12	14–20	55·5
2	23·0	2	3	4	5	10	11–25	35·0	2	3	4	6	10	11–14	73·2
3	20·4	2	3	4	5	9	13–23	49·3	3	4	5	7	11	16–23	97·6
4	20·0	2	4	7	9	12	14–20	67·6	2	4	7	11	14	18–30	79·9
5	19·2	2	3	7	8	13	15–21	93·6	2	4	6	8	13	15–22	61·0
6	16·1	3	6	9	13	30	36–49	35·6	3	6	9	13	28	34–49	38·0
7	14·4	3	8	14	19	28	35–45	32·7	5	11	16	23	30	35–48	46·9
8	13·5	4	9	—	—	—	—	—	5	—	—	—	—	—	—
9	12·5	5	12	—	—	—	—	—	6	—	—	—	—	—	—

These experiments show that the larvae of *C. p. pipiens* are unable to complete their development when the mean temperature is below 14° C. This is also supported by observations which have been made in their natural breeding-places, during September and October. The mean temperature of water in September, in sheltered and in open breeding-places, as observed during the last three years, is 16·20° C. and 14·0° C. respectively. At this temperature the duration of development of this subspecies is from five to six weeks (Table 7). This means that eggs which are laid in September cannot develop to the adult, because the mean temperature of the last week of this month and that of the first week of October is 13·9° C. and 11·4° C. respectively, and is unfavourable for the development of the larvae. This explains the dying of the larvae in September and their complete disappearance towards the end of this month or the beginning of October.

The last generation of adults in England must be produced from eggs which are laid not later than the third or the fourth week of August.

(c) *Salinity of Water.*

Since the polluted water of the breeding-places of *C. p. molestus* has more dissolved salts than the clean water of the habitats of *C. p. pipiens*, it is to be expected that the former subspecies will tolerate much higher salinity than the latter one. In many experiments with different solutions of sodium chloride both subspecies were bred from the eggs, and were fed on finely ground dog biscuit. It has been found that in a solution of 0·75% of this salt both subspecies develop very well and produce normal adults. The highest percentage of development of *C. p. pipiens* was 80 and that of *C. p. molestus* 100. In 1% concentration of sodium chloride, the growth of the larvae is slightly slower and the development is only about 50%. In 1·1% it drops considerably in both subspecies, but is about 100% higher in *C. p. molestus* than in *C. p. pipiens*, which gave only 7·7% of development. Above this concentration the percentage of hatching of eggs of *C. p. pipiens* was very low and all the larvae which hatched were dead on the following day. With the increase of concentration of sodium chloride above 1·1%, the hatching of eggs decreased very sharply, and in 1·4% concentration a few hatching larvae were unable to extract themselves completely from the egg shell, and all were dead in less than six hours.

In a solution of 1·2%, larvae of this subspecies were unable to develop to the adult, but when bred in 0·75% solution, up to the second, third, or fourth stage and then transferred to a 1·3% concentration, 12% of them produced normal adults. This shows that this subspecies is able to adapt itself to an increasing concentration of salts, which may occur in their natural habitats through the excessive evaporation of water.

As regards the development of eggs of *C. p. molestus*, in 1·2% solution of sodium chloride they produce 5·3% of adults, and in 1·3% solution they develop to second stage larvae. The results of these two experiments, and also the higher percentage of development of this subspecies in the other solutions of sodium chloride, indicate that it can resist higher concentrations of salts in water than *C. p. pipiens*.

It has already been mentioned in the description of the larvae that the length of the anal papillae depends upon the concentration of salts in water. It was shown for the first time by Martini (1922) that salt solutions affect the length of the anal papillae of mosquito larvae. This worker came to the conclusion that in several species of mosquito the length of these organs cannot be used as a differential character. Gibbins (1932) found in Africa that the larvae of *C. pipiens* had short, lanceolate papillae in brackish water, whereas the papillae of those from fresh water were long and slender. Wigglesworth (1933a, b and c) found experimentally that the anal papillae of mosquito larvae are water-absorbing organs, and that the absorption is effected by osmosis. He also found that in salt solution the papillae are sloughed off, because their absence is favourable to the larvae in a solution which has a high osmotic pressure.

From the results obtained by the above-mentioned workers it may be assumed that the length of the anal papillae varies proportionally to the concentration of salts in water. In order to test this assumption a series of breeding experiments was performed. The larvae of both subspecies were bred from the eggs in different solutions of sodium chloride and their papillae were measured in the fourth stage.

Figure 7 shows that in a 1% concentration of sodium chloride the papillae of *C. p. pipiens* are only about a quarter the length of those of larvae bred in rain or distilled water. It may be seen in the graph that the length of the papillae

of this subspecies decreases sharply in 0·1%, as compared with the papillae of larvae bred in rain water. Between this concentration and 1·1% the curve is nearly straight. This seems to indicate that the reduction of the length of the papillae is proportional to the concentration of salt in the water. It is quite possible that the curve would have been straighter if the length had been plotted against the osmotic pressure. The curve for *C. p. molestus* does not pass through the points in the graph. This irregular variation in the length

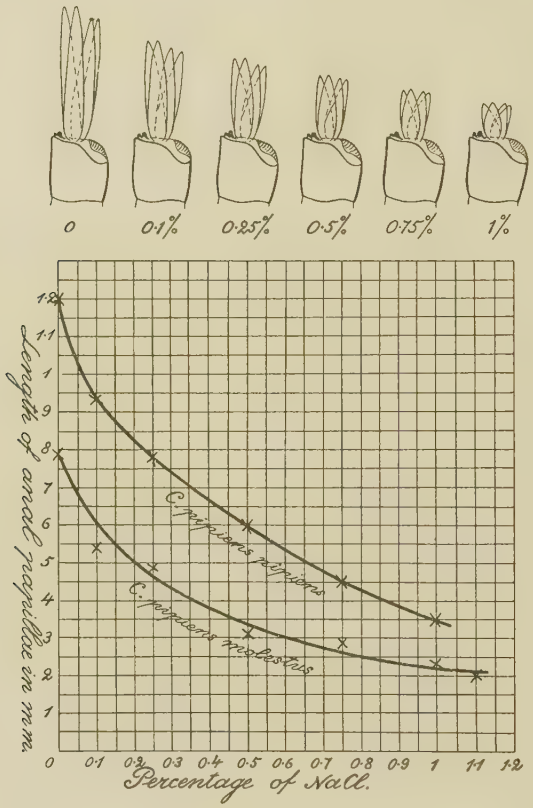

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Fig. 7.—Graph showing the length of the dorsal anal papillae in the two subspecies plotted against the concentration of NaCl solution in which they were bred, and the anal papillae of *C. pipiens pipiens* bred in the same concentrations.

of the papillae of this subspecies was probably due to not using a single raft of eggs, as was done in the experiment with *C. p. pipiens*, but using a different raft for each solution.

It is known that osmotic pressure increases with the temperature, and as the length of the anal papillae depends on the osmotic pressure, it may be expected that larvae which are bred at a higher temperature will have shorter papillae than those which are bred in the same solution, but at a lower temperature. In order to confirm this, two jars were filled with dog-biscuit infusion

made with rain water. Eggs of *C. p. pipiens* from the same raft were introduced into both jars which were kept at different temperatures until the appearance of fourth stage larvae. The mean temperature of the infusion of one jar was 22·0° C. (minimum 17·5° C., maximum 26·0° C.) and that of the other jar, 15·0° C. (minimum 11·5° C., maximum 17·0° C.). On measuring the papillae of the larvae of both jars, it was found that the average length in the larvae of the first jar was 0·95 mm. and in the other jar, 1·03 mm. This showed that in the larvae which were bred at a lower temperature the average length of the papillae was 0·08 mm. longer than in those bred at a higher temperature. In the other experiment, where both jars were filled with 0·75% solution of NaCl, the result was exactly the same as in the first experiment. The average length of papillae of the larvae bred at a higher temperature was 0·37 mm., and that of larvae bred at a lower temperature was 0·45 mm. The average length of the papillae was again 0·08 mm. longer in the larvae bred at a lower temperature.

The results of these experiments prove that the temperature of water affects the length of the anal papillae through the modification of the osmotic pressure, and also show that equal differences of temperature produce equal variations in the papillae irrespective of the concentration of salts in solution.

The long anal papillae in wild larvae of *C. p. pipiens* were more often found in the spring generation, and sometimes also in those collected in the autumn. In the summer generation of larvae the length of the papillae is more often as in those bred in 0·1% of NaCl. The presence of long, slender anal papillae in the spring generation is influenced by the much lower content of salts in the water owing to the more frequent rains, and by the much lower temperature. It has been found that the length of papillae of larva from very polluted water was the same as that of papillae of larvae bred in 0·25%, or in 0·5% concentration of sodium chloride.

The Adults (fig. 8).

The only distinctive character by which these subspecies may be separated from each other is the stricture of the maxillary palps of the males. The first four segments of the palps of the males of *C. p. pipiens* are together longer than the labium, and the third segment is almost straight (fig. 8, *f*). In *C. p. molestus* these segments are as long as or shorter than the labium, and the third segment is usually curved (fig. 8, *e*). The palp of the female of *C. p. pipiens* is shown in fig. 8, *a*, its third segment is pointed and in all the specimens which have been examined, it ends in a cup-shaped sensilla. In females of the Grecian strain of *C. p. molestus* (fig. 8, *b*) the palps have a vestige of a fourth segment (S.4). This vestige has also been found in a very few specimens of the German strain of *C. p. molestus*, but in the majority of females of this strain the vestige of the fourth segment is absent and the third segment has exactly the same structure as that of *C. p. pipiens*.

It has already been pointed out by other workers that the general coloration of *C. p. pipiens* is darker than that of *C. p. molestus*. The dorsum of the thorax of the former subspecies is dark brown; in some specimens it is almost of a sepia colour, whereas in the latter subspecies it is yellowish-brown. In *C. p. pipiens* the dark bands of the tergites, the distal portion of the labium, the dorsal surface of the femora and the tibiae are covered with very dark almost black scales which produces a metallic-blue reflection. When specimens of this subspecies are examined from behind, the creamy-white scales of the distal end of the femora and the tibiae, especially of the middle and the hind legs, are distinctly

seen as white dots, even with the naked eye. But in *C. p. molestus*, owing to the lighter pigmentation of the dark scales, the metallic-blue reflection is indistinct and the yellowish-white scales of the joints of the legs are not visible as white dots to the naked eye.

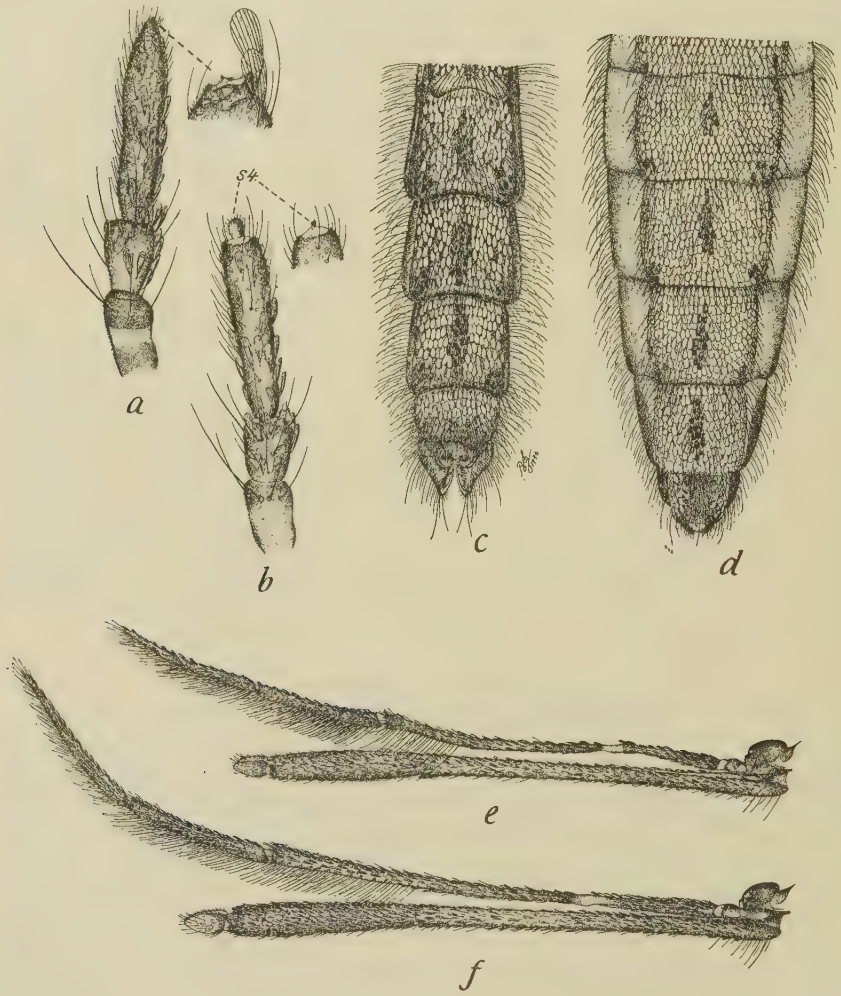

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Fig. 8.—*a*, Palp of female of *C. pipiens pipiens* L.; *b*, same of Grecian *C. pipiens molestus* Forsk. × 125; *b*, Ventral view of abdomen of male; *d*, same of female of *C. pipiens pipiens* L.; *e*, Labium and palp of *C. pipiens molestus* Forsk.; *f*, same of *C. pipiens pipiens* L. × 35.

Another character is present in the sternites, which in *C. p. pipiens* have very distinct median and postero-lateral patches of dark scales (fig. 8, *c*, *d*). The median patches are always present in this subspecies, but the lateral ones

may be either indistinct or completely absent. In *C. p. molestus* the lateral patches are absent. The median ones are usually absent, but may be formed by very few darkish scales. As regards the dark bands of the tergites, their shape presents no distinctive character. They exhibit a considerable variation in both subspecies, but the chaetotaxy of the lobes of the ninth tergite is of some diagnostic value. There are more setae on the lobes of *C. p. molestus* than on those of *C. p. pipiens*. Counts of the setae in 60 specimens of the two strains of the latter subspecies gave the following figures: minimum 6, maximum 11 and mean 8·0, in both sexes. The corresponding numbers for the Grecian and the German strain of *C. p. molestus* were 7, 15 and 10·4. One may use this character to indicate the presence or absence of *C. p. molestus* among specimens, and can only refer those mosquitoes to this subspecies, in which the number of the setae on each lobe is more than 11, since this value represents the maximum number of setae on each lobe of the ninth tergite of *C. p. pipiens*.

An examination of the hypopygia and the pharyngeal pumps in very many specimens of both subspecies revealed no difference in the structure of these parts.

On the basis of the above comparison, the description of each subspecies is as follows:

Culex pipiens pipiens L., 1758.

Culex phytophagus Ficalbi, 1890, 1896.

First four segments of the male palps longer than the labium, the third segment almost straight. Dorsum of the thorax dark brown, in some specimens almost of sepia colour. Distal portion of the labium, dark bands of the tergites and dorsal surface of the femora and the tibiae bear very dark, almost black scales which have a metallic-blue reflection. White scales on the distal end of the femora and the tibiae visible as white dots to the naked eye. Sternites with median and postero-lateral patches of dark scales. The postero-lateral patches may be indistinct or absent. Each lobe of the tenth tergite bears from 6 to 11 setae.

Culex pipiens molestus Forskål, 1775.

Culex molestus Forskål, 1775.
Culex domesticus Germar, 1817.
Culex haematophagus Ficalbi, 1893.
Culex pipiens autogenicus Roubaud, 1933.

First four segments of the male palps as long as or shorter than the labium. Dorsum of the thorax yellowish-brown. Distal portion of the labium, dark bands of the tergites and dorsal surface of the femora and the tibiae bear dark scales having no distinct metallic-blue reflection. Yellowish-white scales on the distal end of the femora and the tibiae not visible as white dots to the naked eye. Sternites of the abdomen without postero-lateral patches of dark scales, the median ones either absent or formed by very few darkish scales. Each lobe of the tenth tergite bears from 7 to 15 setae.

C. p. pipiens is distributed uniformly throughout the Palaearctic region and is probably the only subspecies in the most northern parts of Europe. The adults of this mosquito are more resistant to low temperature than those of *C. p. molestus*, since it has been observed that they are more active below 15° C. than those of the other subspecies. In the south of England the females of *C. p. pipiens* emerge from hibernation in April. Their first rafts appear not earlier than the first or second week in May. Laying gradually increases towards the end of July, and then drops sharply and ceases completely in September. During three years of observations on many breeding-places of this subspecies, only one raft has been found in September, and none in April.

The females begin to enter sheltered places for hibernation in September, though a few specimens may be found in the open as late as the first week of November. The latest swarm of males was observed on the 3rd November, about 4 p.m., when the air temperature was 8·3° C. This swarm disappeared when the temperature dropped to 8·0° C.

The hibernation of this subspecies is apparently governed by low temperature and the shorter duration of daylight, since it has been shown by Tate and Vincent (1932 and 1936) that by using additional illumination, the breeding of this subspecies can be successfully carried on in big cages during the winter.

This subspecies represents the commonest mosquito of rural areas. It has almost completely disappeared from the big towns, with the introduction of drainage for rain water, but is still common in the suburbs, where it breeds in rain-water tubs and tanks.

As regards the distribution of *C. p. molestus*, all records show that it is more common in the Mediterranean parts of the Palaearctic region. In central Europe its distribution is local and it is probably not present in Scandinavia. It is not common in England, where it was found in some seaports, and in some districts of London, close to the Thames. Shute (1933), who recorded the infestation of houses by the man-biting *Culex* in Hull, Harwich and twice in London, was undoubtedly dealing with this mosquito. More recently it has been recorded by Marshall and Staley (1935a and 1935c) in Hayling Island and London. The occurrence of this subspecies in seaports and the absence of any records of it from the interior of the country rather suggests that it is not a native mosquito, but is introduced from time to time from the southern ports of Europe by commerce.

Before the discovery by Roubaud of this subspecies and its habits, all the bites inflicted by this mosquito in this country were attributed to the most common, man-ignoring *C. p. pipiens*. As this mosquito was very numerous everywhere and the cases of annoyance were extremely rare, a belief arose amongst scientific workers that it can only attack man in particular meteorological conditions, such as very warm, calm and sultry weather. Now it is known that all these attacks were made by *C. p. molestus*.

Although a good deal about the behaviour of this subspecies in laboratory conditions is now known, surprisingly little is known about it in its natural habitats. For instance, according to Roubaud it does not hibernate and breeds continuously through the winter. It is quite possible that in the Mediterranean parts of the Palaearctic region, where this subspecies is more common, it breeds all the year round. In central Europe its breeding is more restricted to such places as cellars, cesspits and animal houses. As this subspecies is stenogamus and autogenous, and can also breed in complete darkness (Jobling, 1937), its adults need not leave the above-mentioned places for mating and feeding. Therefore, it is quite possible that it could breed continuously in winter in some of the more protected places of western Europe. But in the eastern parts of Europe the winter is much more severe, and it is rather difficult to believe that this mosquito could survive without hibernation of its females. In connection with this, it should be mentioned here that Reinhard and Gutzevich (1931) recorded man-biting *C. pipiens* from Ukraine. This indicates the presence of *C. p. molestus* in a country where the winter conditions are very severe and absolutely unsuitable for the survival of any stages of this mosquito, with the exception of hibernating females.

The north American *C. pipiens* apparently belongs to this subspecies, since it is a very troublesome pest, invading houses and attacking people at night. The breeding of this mosquito without a blood-meal (autogeny)

and its mating in captivity (stenogamy) were known to Mitchell (1907), who pointed out that bred specimens of *C. pipiens* " which were never allowed to make a meal of blood, mated and laid fertile eggs." The structure of the posterior segments of the abdomen and of the siphon of fourth stage larva, as shown in his figure 34, resembles much more that of *C. p. molestus* than that of *C. p. pipiens*. According to Freeborn (1926) the siphon of the Californian *C. pipiens* is four times as long as its width. This shows that the siphonal index is 4·0. As this value of the index has never been found in *C. p. pipiens*, it means that the Californian larvae were of the *C. p. molestus* type (see Tables 5 and 6). On the other hand, according to Dyar (1928) and Matheson (1929) the siphonal index of the larvae is 5·0, which is the same as in *C. p. pipiens*. It is quite possible that both subspecies are present in America, but it is impossible to say definitely without study of the morphological characters which have been described in this paper and of the habits of the American *C. pipiens*.

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